

FLORAL STRUCTURE AND ANATOMY IN THE FAMILY STYLIDIACEAE SWARTZ.

By R. C. CAROLIN, University of Sydney.

(Twenty-three Text-figures.)

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Synopsis.

The floral structure and anatomy of species of all genera in the family are described. The floral structure seems quite different from that found in Goodeniaceae, although some similarities are noted. Various phylogenetic trends within the family are suggested and its inclusion within the Campanales is questioned.

INTRODUCTION.

Although Mildbraed has dealt with the gross morphology of the flowers of this family fairly exhaustively, little has been published on the microscopic structure. Morren (1838) dealt with the structure of the gynostemium in relation to the trigger movement. Saunders (1939) gives a rather superficial account. Subramanyam (1950, 1951) gives an account of the floral structure of *Levenhookia dubia* and *Stylidium graminifolium*, but he does not deal with vasculature in either.

Details of the techniques used in this investigation will be found in Carolin, 1959.

OBSERVATIONS.

DONATIA.

Two species are recognized; in both, the stamens are free from the style except just at the ovary dome. *D. fascicularis* is a South American species possessing three stamens. Unfortunately no suitable material was available for examination.

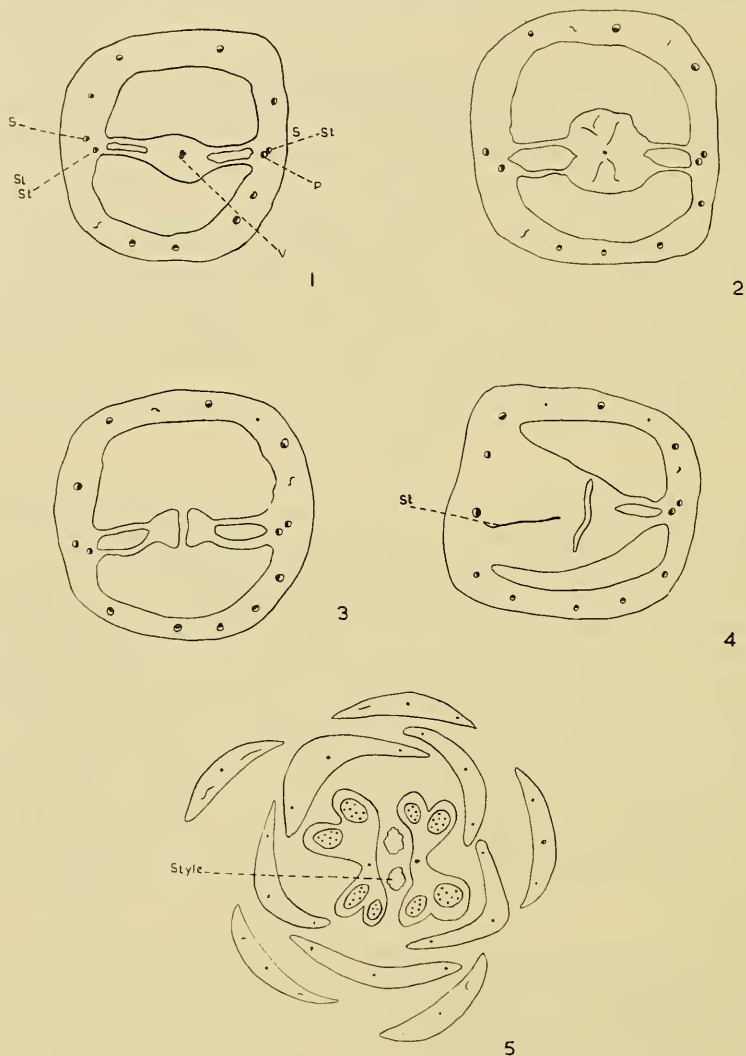
D. nova-zelandiae Hook. f. This species has two stamens only. The divergence of bundles from the receptacular stele may be somewhat irregular. Generally two series of five bundles diverge, one series on the sepal radii somewhat lower than the second on the petal radii. These may branch later so that smaller bundles are found in the pseudo-ovary wall in addition to the ten main cords. Quite low in the pseudo-ovary wall two bundles diverge from the main cords on petal and sepal radii at the junction of the ovary septum and the pseudo-ovary wall (Figs 1, 22). These eventually pass into the stamens. The main cords pass on into the free regions of the floral parts, branching only when these become free from one another. The petal lateral bundles are derived from the petal main bundles and likewise the sepal laterals from the sepal mains (Fig. 5). The stamens are shortly united to the styler base and become free almost immediately. There is apparently no vascular supply in the style itself which bifurcates near the ovary dome.

After the divergence of the main cords to the pseudo-ovary wall the receptacular stele is resolved into a single bundle with a central xylem mass and irregular patches of phloem surrounding it. This passes into the ovary septum which consists of two sheets of parenchymatous tissue on either side of a solid core of placenta and connecting this latter to the ovary wall (Figs 1, 2). Thus the ovary is bilocular in this region, where the ovules are attached. The vascular strand in the placental axis is completely used up in supplying the ovules. Just above the highest ovule insertions a split appears in the central (sterile) axis and the ovary appears unilocular (Fig. 3). Immediately beneath the ovary summit the two halves meet once again to produce another bilocular zone. The ovary dome appears to be generally, although weakly, nectiferous (Fig. 17).

PHYLLOCHNE.

P. colensoi Berggren. A varying number of bundles (about ten) separate from the receptacular stele almost together. They pass upwards into the pseudo-ovary wall. The

bundles supplying the six petals and six sepals are resolved in no apparently regular order from these cords. In the cortex of the receptacle the two lateral cords divide and the inner members pass upwards into the gynostemium (Figs 6-10). They are, apparently, the staminal bundles, as they supply the two bilocular anthers on either side of the stigmatic lobes. The stigmata receive no vascular strands at all.



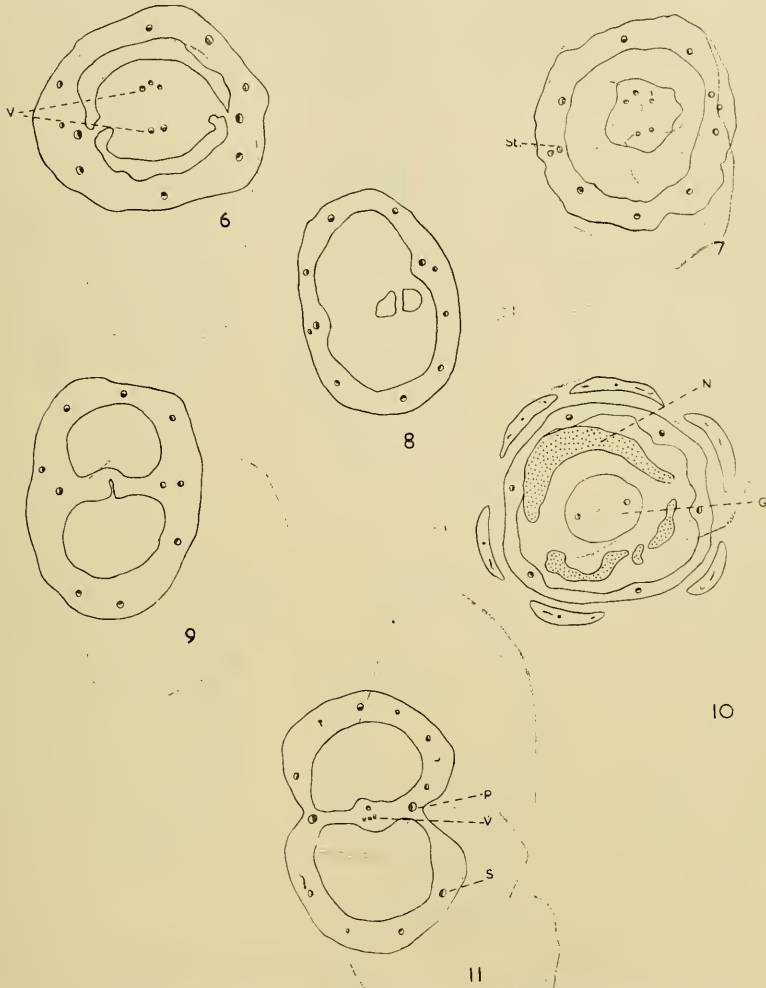
Figs 1-5. *Donatia nova-zelandiae*.—1. Pseudo-ovary, lower zone, below ovular insertion; 2. pseudo-ovary: zone of ovular insertion; 3. pseudo-ovary: "unilocular" zone; 4. pseudo-ovary: upper "bilocular" zone; 5. flower above ovary. $\times 20$.

Above the divergence of the cords to the pseudo-ovary wall, the receptacular stele, consisting generally of five bundles, passes into the enlarged placental axis (Fig. 6). The ovary is bilocular in this zone. Higher up, the septum aborts on either side of the placental axis and the ovules are attached in this unilocular region (Fig. 7). The vascular tissue is completely used up in supplying the ovules inserted on this free central placenta. Above the ovular insertions the axis splits into two halves (Fig. 8). These strands are unvascularized and they eventually join together, and to the ovary

wall, to regenerate an apparently bilocular condition (Fig. 9). There is a double, somewhat irregularly lobed nectary at the base of the gynostemium on the ovary dome. No vascular bundles were observed to enter it.

FORSTERA.

Similar in all respects to *Phyllachne*.



Figs 6-10. *Phyllachne colensoi*.—6, Pseudo-ovary: lower “bilocular” zone below ovular insertion; 7, pseudo-ovary: “unilocular” zone showing free central placentae; 8, pseudo-ovary: upper zone of ovary showing sterile parenchymatous strands; 9, pseudo-ovary: uppermost “bilocular” zone; 10, flower above ovary. $\times 20$.

Fig. 11. *Stylidium graminifolium*.—Pseudo-ovary: lowermost zone below ovular insertion. $\times 16$.

OREOSTYLIDIUM.

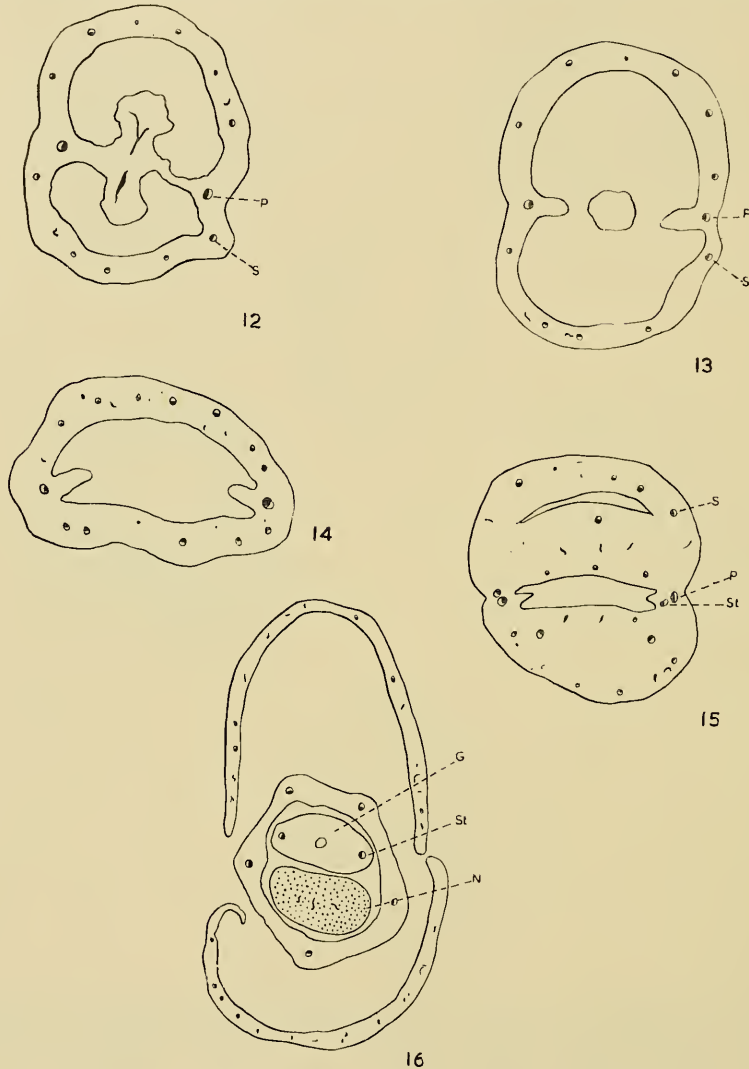
Similar to *Phyllachne* except for the absence of the sterile strands connecting the placental axis to the ovary summit and the apparently bilocular condition in the region of ovule insertion.

STYLIDIUM.

Unfortunately no species of the section *Forsteropsis* were available for study. Mildbraed (1908), however, gives fairly clear illustrations of some of the member species. The gynostemium is of a rather specialized type, whereas the ovary shows some features

which can be considered primitive. Notable in this respect are the two parenchymatous strands attached to the placental axis, as in *Phyllachne*, but apparently free from the ovary summit.

S. graminifolium Swartz. In the receptacle ten bundles diverge from the central stele, five on the sepal radii somewhat lower than the other five on the petal radii. The



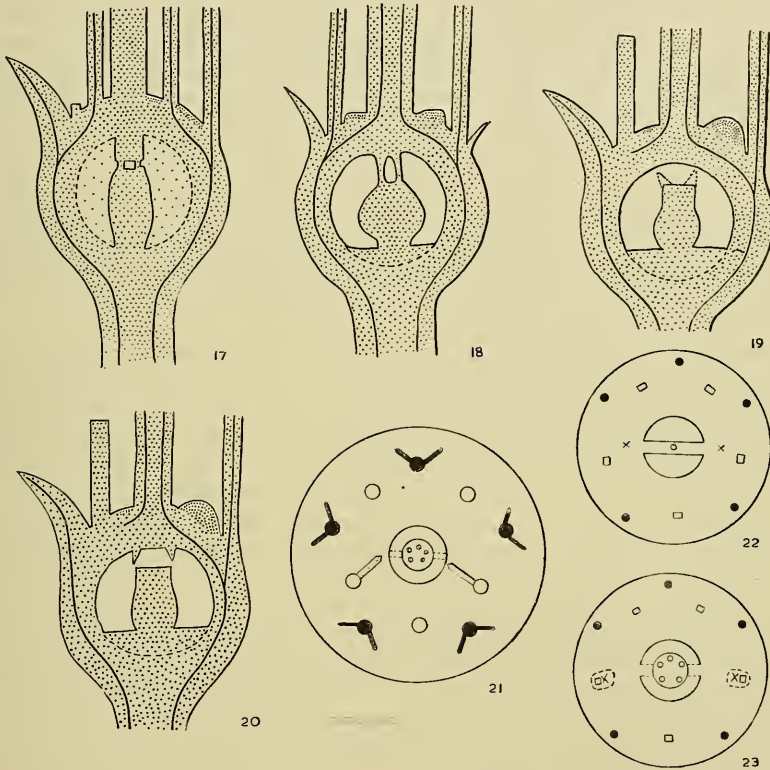
Figs 12-16. *Stylidium graminifolium*.—12, Pseudo-ovary: zone of ovular insertion; 13, pseudo-ovary: "unilocular" zone showing (sterile) free central placentae; 14, pseudo-ovary: upper zone; 15, ovary dome; 16, flower above ovary. $\times 16$.

residual stele also consists of five bundles. The ten main cords in the pseudo-ovary wall give off smaller branches irregularly, which form a network throughout the wall, but the number of main cords remains constant (Figs 12-14). At the ovary dome most of these outer bundles give off weak strands which converge upon the base of the gynostemium. Those strands in the posterior position fade out, whereas those in the

Key to Figures 1-16—S, Sepal main bundle or cord in pseudo-ovary wall on sepal radius. P, Petal main bundle or cord in pseudo-ovary wall on petal radius. St, Staminal bundle. G, Gynostemium. V, Placental bundle(s). N, Nectary.

anterior position are diverted into the large nectary at the base of the gynostemium (Figs 15, 16). Also at the ovary dome the bundles supplying the anterior-lateral petals distribute one large trace each into the gynostemium. This represents the sole supply to the anthers; no vascular tissue, apparently, is distributed to the stigmata (Figs 15, 16, 21, 23).

The placental supply is derived from the five bundles remaining in the receptacle after the divergence of the cords to the pseudo-ovary wall. The anterior two and the posterior three amalgamate, in that combination, to form two strands which pass into the placental axis. These bend horizontally into the two swollen placentae, branch



Figs 17-20.—Diagrammatic, lateral, longitudinal sections of pseudo-ovaries: 17, *Donatia*; 18, *Phyllachne*; 19, *Styloidium*; 20, *Levenhookia*.

Fig. 21.—Generalized plan of the distribution of vascular bundles at the ovary dome of *Styloidium*.

Figs 22, 23.—Diagrammatic transverse sections of pseudo-ovaries: 22, *Donatia*; 23, *Styloidium*.

profusely, and are totally used up in supplying the ovules. Throughout most of the region of ovular insertion the septum and placental axis divides the ovary into two loculi. At the upper part of this region the septa part from the placental axis on either side, leaving a free central column which is sterile in its upper part and free from the ovary summit (Figs 12, 13, 19). The inturned edges of the abortive septa remain quite apparent (Figs 14, 15).

S. laricifolium Rich. Very similar to the preceding species.

S. adnatum R.Br. This species was not examined in the present investigation, but it is mentioned here as an example in which one of the loculi is almost completely aborted (Saunders, 1939).

In many species illustrated by Mildbraed (1908) the septa have apparently completely aborted and the ovules are borne on free-central placentae. However, he also pictures *Phyllachne* as showing this condition, whereas the septa are present but very low in the ovary. The same situation may apply in some, at least, of the *Stylidium* species so figured.

LEVENHOOKIA.

L. dubia Sond. in Lehm. With regard to vasculature and structure of the ovary this species is similar to *Stylidium*. The septa are complete at the base of the ovary, but almost immediately lose contact with the placental axis. Ovules are inserted in the free-central region only. At the top of the loculus the inturned margins of the abortive septa rejoin, so that it appears that two parenchymatous sheets project downwards from the ovary roof but without making contact with the placental axis. Thus the uppermost, divided region of the ovary is present in this species although absent in *Stylidium*. Subramanyam (1950) figures this, but contents himself with calling it a "structure" and does not attempt to interpret it (Fig. 20).

DISCUSSION AND CONCLUSION.

The family is rather more uniform than the Goodeniaceae. The changes of the floral structure are mainly concerned with the loss of the septa connecting the placental axis to the ovary wall, with the condensation of the vascular supply, and with the union of the stamens and style into a gynostemium. These trends are summed in Figures 17, 18, 19, 20, 22 and 23.

Donatia is clearly the most primitive member of the family. The stamens are free from the style, the ovary septum is complete except for a very small zone near the summit, and the staminal vascular supply is free for the greater part of the length of the pseudo-ovary wall. The ovary, then, is directly comparable with that of the Goodeniaceae, showing the same three vertical zones (Carolin, 1959). It is noted that even in this genus the style is not supplied with vascular tissue.

In all the other genera the stamens and style are united into a gynostemium and staminal strands are united to the adjacent main cords in the pseudo-ovary wall (Figs 18, 19).

The ovary shows a phylogenetic progression to the unilocular condition, but in a different direction from that of the Goodeniaceae. In the latter case it is due to splitting in the axis itself, indicating how parietal placentation may arise from axile, although it does not actually occur (Carolin, 1959). In the former case it is due to the separation of the septum on either side of the swollen placental axis leaving a free-central placenta. In *Phyllachne* this septal abortion leaves two strands connecting the axis with the ovary summit (Fig. 18). These represent the two thickened ends to the septa in the medial zone of *Donatia* (Figs 3, 17). In *Stylidium* sect. *Forsteropsis* these strands have lost their connection with the summit; in other *Stylidium* spp., they have aborted altogether; and in *Levenhookia* they have lost their connection with the placental axis (Figs 19, 20). Through *Stylidium* and *Levenhookia* there is a progressive shortening of the septate zone until the placenta appears quite free, but there seems to be no progression to a reduction in the number of ovules as in Goodeniaceae (Carolin, 1959).

The vascular supply to the placenta of *Phyllachne* (Figs 6, 7) and *Stylidium graminifolium* suggests that the ovary is derived from five carpels, the five central bundles remaining as discrete entities, often into the placental axis (Fig. 11). There are no vascular supplies to the style or stigmata; therefore there is no further evidence in this direction. It can be suggested, then, that the loculi of the ovary, when they are present (pseudo-carpels), are compounded one of two and one of three carpels, although it is impossible to decide the position of these morphologically different carpels due to the absence of carpel dorsal strands (Fig. 21).

The same considerations with regard to the pseudo-ovary wall apply in this case as in the Goodeniaceae (Carolin, 1959).

The nectary, which, as in the case of Goodeniaceae, may be derived from the ovary wall, shows a progressive concentration to an anterior position. In *Donatia* the summit of the ovary is nectariferous and in *Phyllachne* the nectary is a double, irregularly lobed structure in that position (Curtis, 1946). In *Stylidium* there is a large, domed protuberance on the ovary dome in the anterior position and a much smaller one posteriorly. In all species, except one, there is no vascular supply to the nectary, implying that it has no relationship with aborted floral organs. Only in *Stylidium graminifolium* is there a weak and irregular supply of xylem and phloem derived from the network of bundles which passes below the nectary and ends in the base of the gynostemium in other species (see Subramanyam, 1951). A vascular supply may have been diverted from its normal path by some intense gradient operating at the critical time, possibly an increase in sugar and water requirements of the nectary. This may indicate how it is possible for the direction of a bundle to be changed in the phylogenetic sense.

Rapson (1952-1953) has maintained the separation of the Donatiaceae from the Stylidiaceae on the grounds of anatomical differences in parts other than the flower. In view of the plausibility of interpreting the flowers of *Donatia* as the basic type of the family, in the phylogenetic sense, it seems unprofitable to divide the family as recognized by Mildbraed (1908).

Various other authors have suggested that *Donatia* shows affinities with the Saxifragaceae; indeed many systematists have placed it in that family, e.g., Bentham and Hooker in the "Genera Plantarum". Both the superficial construction of the flower and the vegetative appearance point to such a relationship. The family, however, seems to be a natural unit, possibly showing affinities with Campanulaceae or Saxifragaceae (those Saxifragae with an inferior ovary). These two groups are so different that it seems unlikely that a dual relationship is possible. Rapson decided that his anatomical studies indicated a Campanalian affinity, but his evidence is slender and nowhere does he attempt a critical comparison with the anatomy of *Saxifraga*. Mildbraed gives much weight to the occurrence of inulin in *Stylidium* and in many members of the Campanales. But, as Rapson points out, inulin has too wide a distribution in the Angiosperms for its presence to be of much phyletic value.

The structure of the ovary of Stylidiaceae belongs to the same general pattern as that of the Campanales (Carolin, 1959, unpub.), but this pattern is not uncommon in other groups and can be given little weight. Indeed, Saunders (1939) indicates that the ovary of *Saxifraga* is bilocular below and unilocular above. Union of the bases of the styles of this genus would produce the situation found in *Donatia*.

Subramanyam (1951) gives a list of similarities with regard to the embryo-sac and embryo morphology, but most of these characteristics are also widely distributed. He also says: "*Stylidiaceae* . . . resembles *Lobeliaceae* in having zygomorphic flowers and confluent anthers." At least three genera within the family have actinomorphic flowers and the anthers are not strictly connate (certainly not in *Donatia*), but are adnate to the style.

The glandular hairs present in many of the Stylidiaceae are found elsewhere in the Campanales only in Goodeniaceae, although they occur commonly in *Saxifraga* (Engler, 1916-1919). Also tannin cells occur commonly in Stylidiaceae (also see Rapson, 1952-1953) and in Saxifragaceae (Metcalf and Chalk, 1950), but are uncommon or even absent in Campanulaceae.

The systematic position of the family is obscure. Indeed, a consideration of the pollen-presentation structures, which will be published separately, suggests even more strongly that the affinities may not be with the Campanales. More evidence with regard to the Saxifragaceae is needed before the position of Stylidiaceae can be further determined.

Professor W. R. Phillipson, Professor N. S. Bayliss and Miss B. J. Briggs have collected material which was used in this investigation. The collection of the rest was made possible by a research grant from the University of Sydney.

VOUCHER SPECIMENS EXAMINED.

Phyllachne colensoi (Hook. f.) Berg., Mt Rufus, Tasmania. B. Briggs 1.1958. SYD. *Forstera bellidifolia* collected by Miss B. G. Briggs. No voucher. *Donatia nova-zelandiae* Hook. f., collected by Prof. N. S. Bayliss. No voucher. *Stylidium graminifolium* Swartz, Oatley, W. J. Peacock, Jan. 1958. SYD. *Stylidium laricifolium* Rich., Khyber Pass, N.S.W. R. Carolin, no/589. 6.10.1957. SYD. *Levenhookia dubia* Sond. in Lehm., Triangle Res. Brackleeby, N.S.W. E. J. McBarron, no. 4952, 25.9.1950. SYD.

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